

New anatomical information on *Holonema* (Placodermi) based on material from the Frasnian Gogo Formation and the Givetian-Frasnian Gneudna Formation, Western Australia

Kate TRINAJSTIC

Department of Geology and Geophysics, University of Western Australia,
Stirling Hwy, Nedlands 6009, Western Australia (Australia)
ktrinajs@mail.geol.uwa.edu.au

Trinajstic K. 1999. — New anatomical information on *Holonema* (Placodermi) based on material from the Frasnian Gogo Formation and the Givetian-Frasnian Gneudna Formation, Western Australia. *Geodiversitas* 21 (1) : 69-84.

ABSTRACT

Additional specimens of the arthrodire *Holonema westolli* Miles, 1971 from the Late Devonian Gogo Formation, Canning Basin, Western Australia enables elements from the post-thoracic armour – namely the vertebral column, the pelvic girdle, the pelvic fins and the squamation – to be described. The species diagnosis is improved by including this new anatomical information. Comparison of *H. westolli* scales with isolated scales recovered from the upper beds of the Gneudna Formation permits these isolated scales to be referred to the species *H. westolli*. Interspecies differentiation in scale ornamentation allows the identification of *Holonema* species on the basis of scale morphology in the absence of body plates.

KEY WORDS

Holonema westolli,
vertebrae,
scales,
Gogo,
Gneudna,
Devonian,
Australia.

RÉSUMÉ

Nouvelles données anatomiques sur Holonema de la Formation Gogo (Frasnien) et de la Formation Gneudna (Givétien-Frasnien) d'Australie occidentale.

La découverte de nouveaux individus de l'arthrodire *Holonema westolli* Miles, 1971 dans la formation dévonienne Gogo dans le bassin Canning, en Australie occidentale, a permis la description d'éléments vertébraux des régions abdominale et caudale antérieure, ainsi que des éléments dermiques, pelviens et des écailles. La diagnose spécifique est amendée en conséquence. La comparaison intraspécifique à partir des écailles de *H. westolli*, permet l'identification de différentes espèces d'*Holonema* en l'absence d'éléments dermiques significatifs.

MOTS CLÉS

Holonema westolli,
vertèbres,
écailles,
Gogo,
Gneudna,
Dévonien,
Australie.

INTRODUCTION

Placoderm plates have been important elements in biostratigraphic studies (Young 1974; Lelièvre *et al.* 1986), however the numerous micro-vertebrate remains have proved difficult to identify, and thus their biostratigraphic use has been limited. Although scale cover is known in all placoderm orders except the Phyllolepidia it is rarely preserved (Denison 1978). This makes reliable identification of forms difficult in deposits where only isolated scales are recovered, with many placoderm scales being referred to the "bucket" genus "*Ohioaspis*" Wells, 1944. Recently attempts have been made to classify isolated scales and subdivide the genus "*Ohioaspis*." Turner & Murphy (1988) suggested Australian scales classified as *Ohioaspis* may in fact be buchanosteid scales. Burrow (1996) has identified ten placoderm scales and erected two new Early Devonian form taxa, *Kadunglepis serrata* Burrow, 1996 and *Jerulalepis picketti* Burrow,

1996 based on their distinctive ornament and histology, from the Trundle Beds, Gleninga Formation and Jerula Formation of NSW Eastern Australia. Only recently in Australia have isolated scales been related to articulated plates. These descriptions, in addition to placoderm scales already known from northern hemisphere sites (Table 1), presents the possibility that in the future, placoderm body scales may be useful biostratigraphic indicators for Devonian sequences.

One of the most urgent tasks in achieving the full biostratigraphic potential of placoderm scales is the description of known taxa with scale cover. It is therefore the aim of this paper to describe the scales of the Devonian holonemauid, *H. westolli* Miles, 1971 from the Gogo Formation, Western Australia, thus providing a uniform reference for the identification of isolated *Holonema* scales from the Devonian. Although this species is well-known from excellently preserved head and thoracic armour (Miles 1971), the vertebral

		EUROPE	AUSTRALIA	CHINA	MIDDLE EAST	USA
DEVONIAN	Fam			<i>Remigolepis</i>	<i>Remigolepis</i>	<i>S. kepleri</i>
	Fras	<i>H. radiatum</i>	<i>H. westolli</i>		<i>H. radiatum</i>	
	Giv	<i>A. magna</i> <i>Pterichyodes</i>	<i>B. gippslandensis</i> <i>B. cujodensis</i> <i>B. ferruginosa</i>			<i>Ohioaspis</i>
	Eif	<i>Ohioas</i> <i>Actinolepis tuberculata</i>	<i>Australanema</i> <i>Mitaoonaspis</i>			
	Ems	<i>Lunaspis</i> <i>Germundina</i> <i>Buchanosteid</i>	<i>Ohioaspis</i> <i>Ghodradobeeon</i> <i>Wutaonaspis</i>	<i>Lunaspis</i> <i>Buchanosteid</i>	<i>Stensioella</i> <i>Buchanosteid</i>	
	Pra	<i>A. spinosa</i>	<i>Kadunglepis serrata</i> <i>Jerulalepis picketti</i> <i>Buchanosteid</i>	<i>Buchanosteid</i>		
	Loch					

TABLE 1. — Stratigraphic distribution of some Devonian placoderms in which the squamation is known.

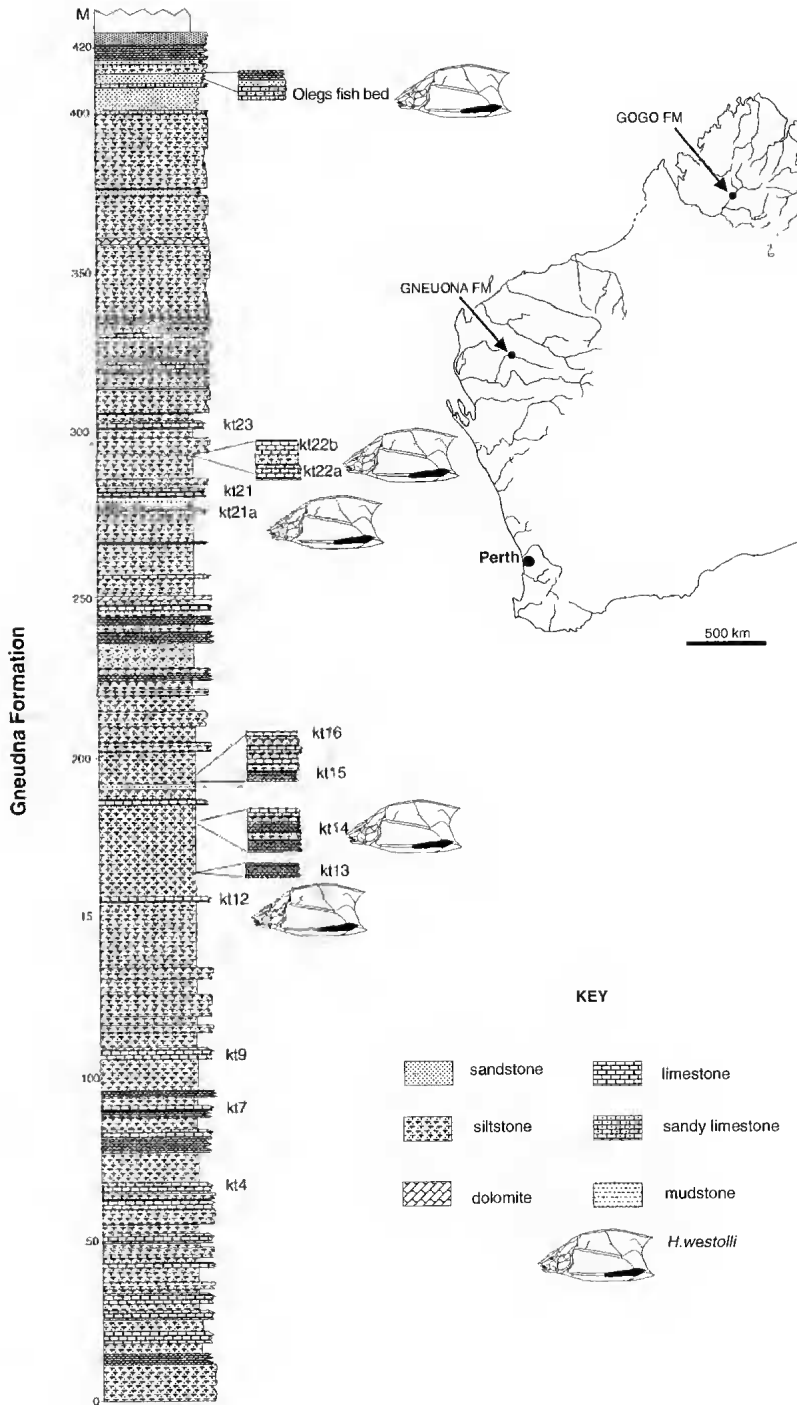


FIG. 1. — Stratigraphic column indicating the beds in which *Holonema westolli* occurs in the Gneudna Formation and map of Western Australia showing the location of the Gneudna Formation and the Gogo Formation.

column, pelvic girdle and squamation, have until now, remained unknown. From this description it is hoped that a reliable identification and taxonomic study of isolated placoderm scales from the Gneudna Formation, Carnarvon Basin, Western Australia will be made (Fig. 1).

MATERIALS AND METHOD

The study is based on two specimens of *H. westolli* from the Frasnian Gogo Formation, Western Australia, and isolated scales from the late Givetian-early Frasnian Gneudna Formation, Williambury Station, Western Australia. All specimens described in this paper are deposited in the palaeontology collections of the Western Australian Museum (WAM), Perth, Western Australia.

WAM 95.6.111 (in part and counterpart) (Figs 2A, B, 4A, B): the only plate preserved from the body armour is an undistorted posterior region of the posterior ventrolateral plate (PVL, fig. 4A). The vertebral column seems to have been pushed through the skin and is suggestive of dorsal ventral flattening prior to nodule formation. The specimen is approximately symmetrical about the sagittal section and in cross section approximates the real body. Two pelvic bones, and squamation showing the pelvic fin outline are also preserved.

WAM 96.12.2 consists of an incomplete vertebral column, part of the squamation and one pelvic bone.

WAM 97.7.1 consists of ten isolated scales from Beds 22 and OFB (Olegs Fish Bed) from the Gneudna Formation.

WAM 97.7.2. is a single scale from Bed 22 of the Gneudna Formation.

WAM 97.7.3. is a single scale from Bed 14 of the Gneudna Formation.

All specimens were acid prepared in 10% acetic acid (Rixon 1979) except for part A of specimen 95.6.111 which has been set in resin. Scales and vertebral elements described in this paper come from the residue of limestone samples treated with acetic acid. Scanning electron micrographs were taken on a Philips 505 scanning electron microscope.

SYSTEMATIC DESCRIPTION OF SQUAMATION AND POST-THORACIC ARMOUR SKELETON

Family HOLONEMATIDAE Obrutchev, 1932
Genus *Holonema* Newberry, 1889

Holonema westolli Miles, 1971

HOLOTYPE. — WAM 70.4.243 a complete body armour of 35 cm with tooth plates from the Frasnian, Gogo Formation, Gogo Station, Western Australia. The holotype has been figured photographically in Miles (1971, fig. 73).

DESCRIPTION OF POST-THORACIC ARMOUR

Vertebral column

(Figs 2A, B, 3A-G, 4A, B, 5A-C)

The vertebral column of *H. westolli*, comprises opposed, paired, perichondrally ossified neural and haemal elements with no spines, which sit upon an unrestricted notochord. Unlike the other Gogo placoderms, such as *Torosteus* Gardiner *et* Miles, 1990, where the two neural arches and two haemal arches are fused (Denison 1978), the vertebral elements of *H. westolli* remain unattached, although closely opposed, along the length of the vertebral column. Regional variation is seen in the vertebral column of WAM 95.6.111 with twenty-four anterior vertebral elements and a minimum of eighteen caudal vertebral elements distinguished (Figs 2B, 5C). The caudal elements start at the posterior margin of the pelvic fins. There is a short transition zone at the level of the pelvic fins. The lateral cavity on the anterior vertebral elements (Figs 3A-E, 4B) is wide and becomes narrower towards the caudal region (Figs 2A, 3G). The paired abdominal vertebral elements comprise thin plates of transversely arched bone (Figs 2B, 3A-E). There is a thin flange (fln) of bone that projects medially from the left and right elements (Figs 3A, D, G). The left and right bony flanges are closely opposed but do not fuse (Fig. 2A, B). On the internal medial surface is a shallow groove (grv, Fig. 3A, B, D, H) for the nerve cord. Anteriorly and posteriorly there seems to be articulation surfaces on the vertebral elements (Fig. 3E). It cannot be ascertained

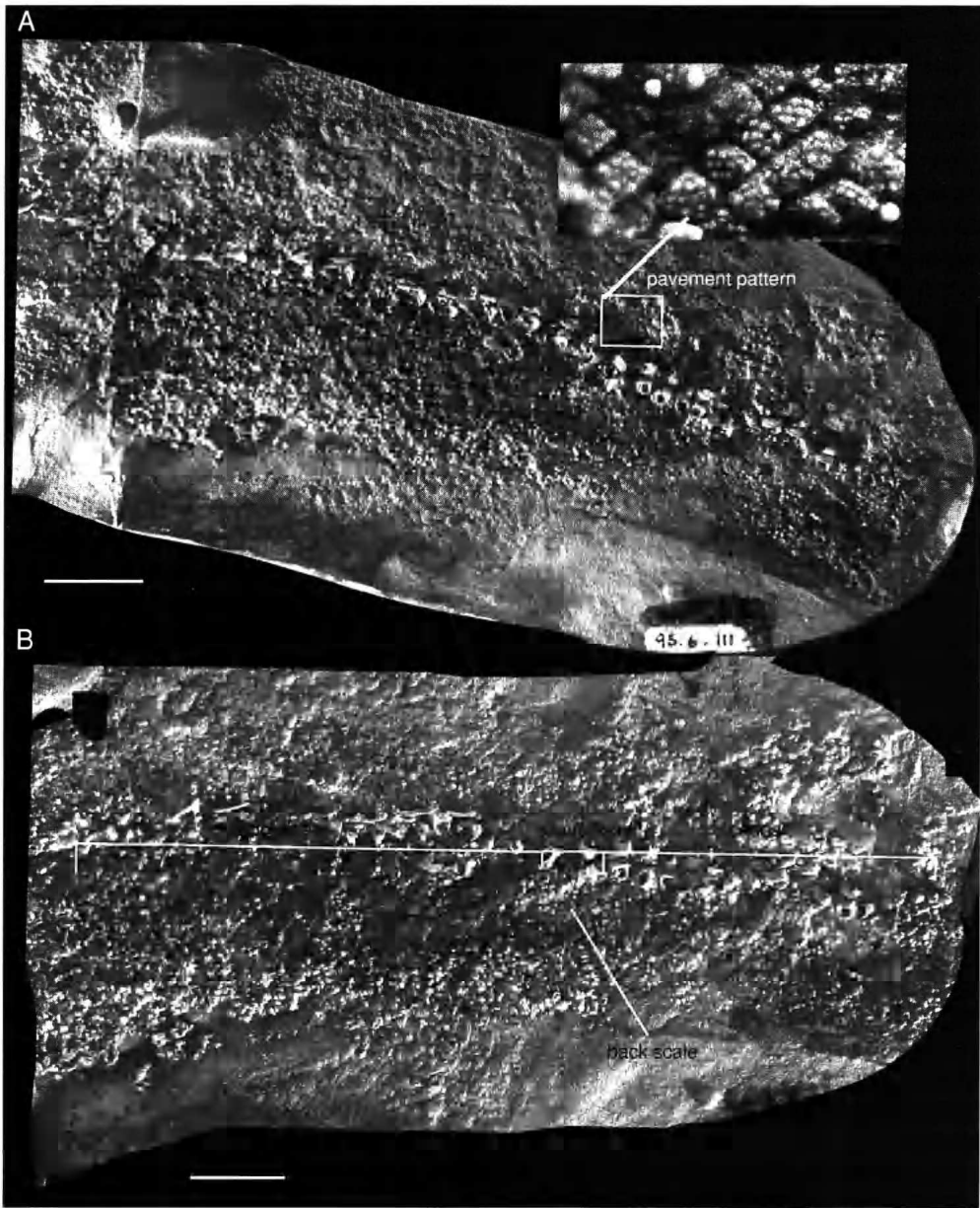


FIG. 2. — *Holonema westolli* (WAM 96.6.111A), tail region; **A**, pavement pattern of scale arrangement; **B**, division of the vertebral column and position of large dorsal back scale. Scale bars: 2 cm.

with certainty whether these articulation surfaces provided articulation between vertebral elements or were the sites of attachment for cartilaginous neural and haemal spine elements. The caudal vertebrae also have a central medially projecting flange of bone (fln, Fig. 3G). The flange of bone is more developed in the caudal vertebral ele-

ments than in the anterior vertebral elements, but like the anterior vertebral elements the flanges of the right and left elements do not fuse. **Remarks.** In *H. westolli*, it appears that there were no neural and haemal spines on the anterior vertebral elements. A similar condition is seen in the vertebral elements immediately below the

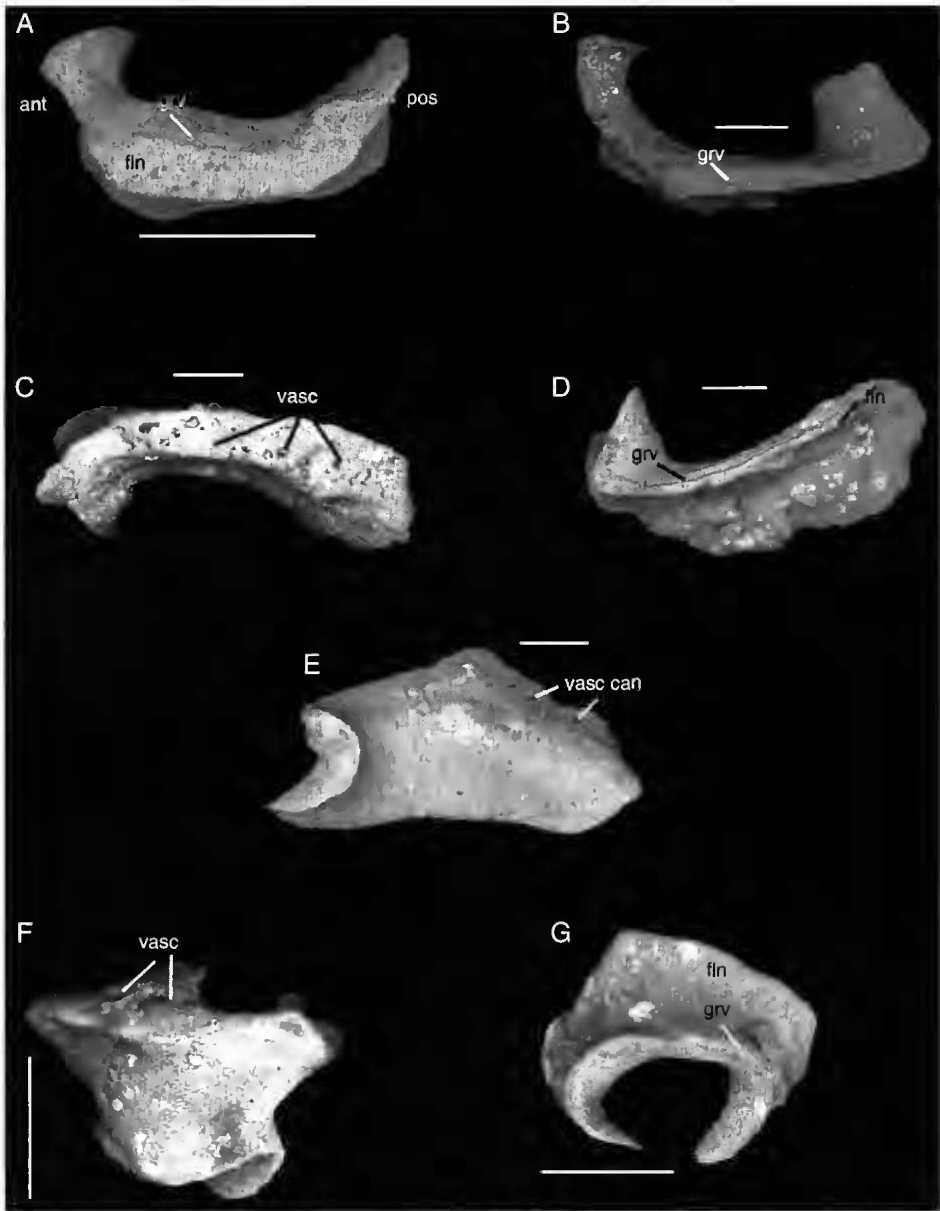


FIG. 3. — *Holonema westolli*. A-E, WAM 96.12.2, abdominal vertebral elements; F-G, BMNH (unregistered), caudal vertebral elements; ant, anterior; fln, flange of bone; grv, groove for nerve cord; pos, posterior; vasc, vasc can, vascular canal. Scale bars: 1 mm.

median dorsal plate in *Incisoscutum ritchiei* (Dennis *et* Miles, 1981). However, the abdominal and caudal vertebrae of *Incisoscutum ritchiei* do possess neural and haemal spines. In *Cocosteus cuspidatus* Miles *et* Westoll, 1968 (fig. 48), *Eastmanosteus calliaspis* Dennis-Bryan, 1987 and *Compagopiscis croucheri* Gardiner *et* Miles, 1994

the neural and haemal arches of the body region are fused into perichondrial ossified spines. It is suggested that there were cartilaginous neural and haemal spines in the caudal region of *H. westolli* as there is considerable narrowing of the lateral cavity in the caudal region suggesting different muscular attachment from the anterior region of

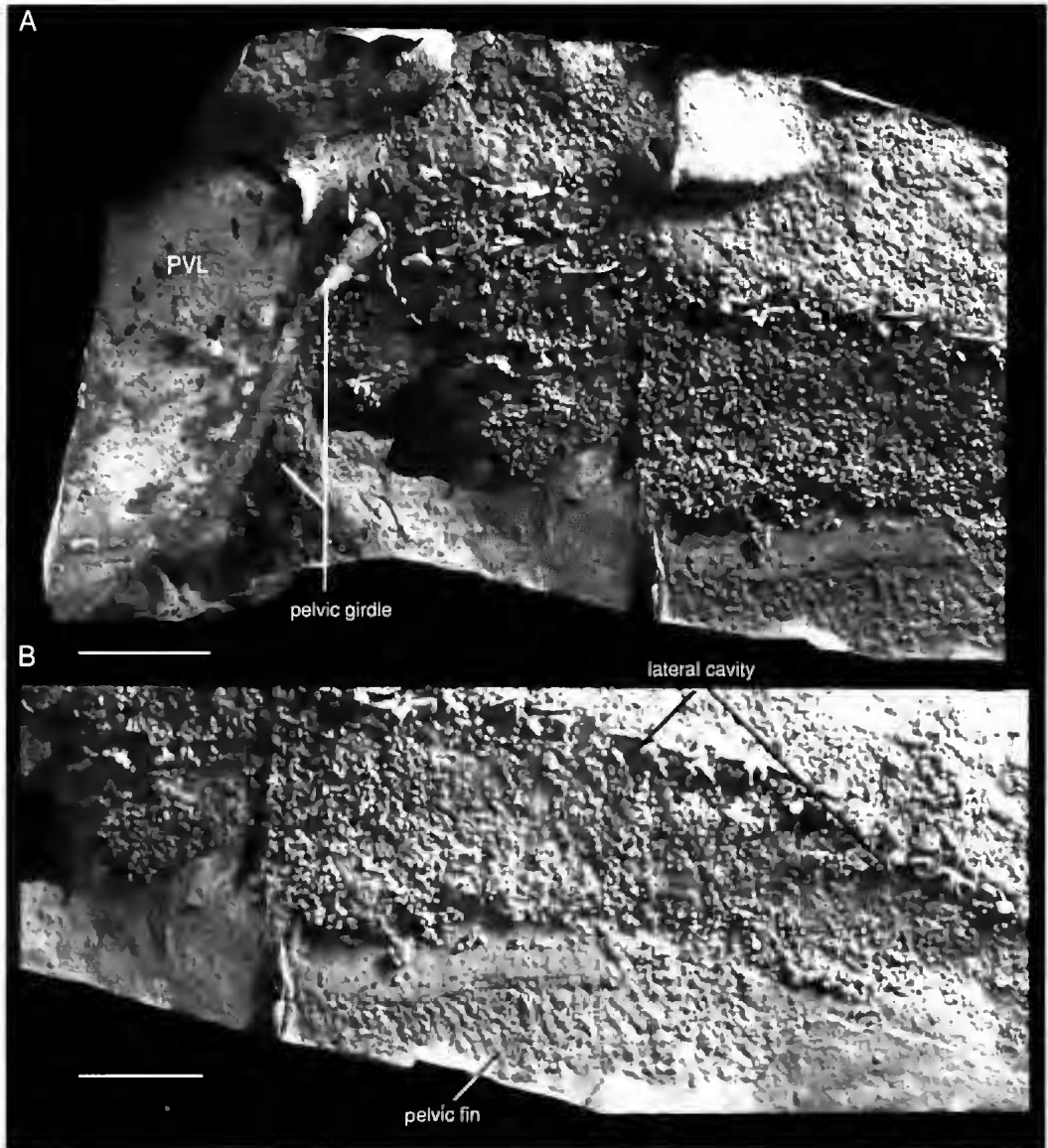


FIG. 4. — *Holonema westolli* (WAM 96.6.111A); A, posterior region of the trunk armour showing the relationship of the pelvic girdle to the PVL (Posterior ventro-lateral plate); B, outline of the pelvic fin and scale rows along the pelvic fin. Scale bars: 2 cm.

the vertebral column. The presence of neural spines in the caudal region would provide increased mechanical leverage for muscles in the tail which are important when acceleration of the tail is greater than acceleration in the body.

Pelvic girdle and fins (Figs 4A, B, 5A-C)

The bony, pelvic girdle of *H. westolli* (95.6.111)

consists of broad, left and right lateromedially flattened iliac processes lying immediately behind the posterior ventrolateral plate (Fig. 4A). The iliac processes taper sigmoidally and project posterodorsally (Fig. 4A). The left process appears to be reversed, whereas the right process appears to be in the position held during life, where they would have been joined in the midline.

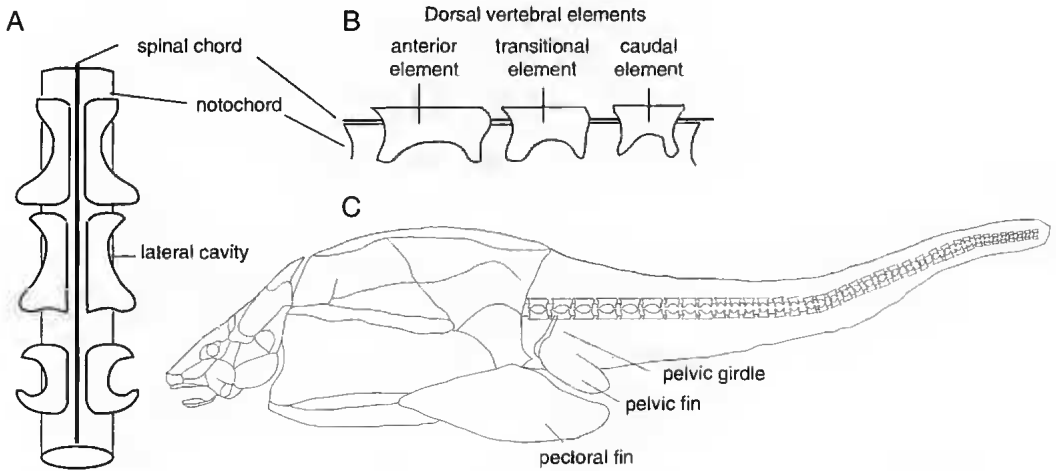


FIG. 5. — *Holonema westolli* (WAM 96.6.111A); A, reconstruction of the vertebral elements in dorsal view; B, reconstruction of the vertebral elements in lateral view; C, reconstruction showing the position of the vertebral elements, the pelvic girdle and the pelvic and pectoral fins.

The outline of the pelvic fins is preserved in WAM 95.6.111 (Fig. 4B). They appear semi-circular in outline, resembling the condition in Stensioellida and Rhenanida (Denison 1978). As in Rhenanida, the pelvic fins are positioned close behind the large pectoral fins (Fig. 5C). The pelvic fins are covered with scales on both the dorsal and ventral sides. The scales decreased in size proximo-distally as in *Rhamphodopsis* Watson, 1934 and *Rhynchodus* Newberry, 1873. No fin radials have been preserved in either specimen of *H. westolli* however, the scales seem to be arranged in approximately thirty proximo-distal rows (Fig. 4B).

Remarks. The position of the pelvic elements immediately behind the posterior ventral plate is suggestive of the pelvic fins being closely situated behind the pectoral fins. This position is further forward than in earlier reconstructions of *H. westolli* (Long 1991a, 1995) and is seen in *Sigaspis* Goujet, 1973 where it is considered by Denison (1978) to represent the less derived condition. The absence of a basal plate in *H. westolli* is unlike the condition in the eubrachythoracoid arthrodires where a perichondrially ossified basal plate is seen in *Camuropiscis* Dennis et Miles, 1979 *Coccosteus cuspidatus* Miles et Westoll, 1968, *Incisoscutum richiei* (Dennis et Miles, 1981) and *Fallacosteus* Long, 1988. The absence of a perichondrially ossified basal plates is also

considered to represent the less derived condition (Long 1988).

The presence of scales on both the dorsal and ventral sides of the pelvic fins and the arrangement of the scales into proximo-distal rows in *H. westolli* is similar to the condition noted in *Rhamphodopsis* and *Rhynchodus* by Stensiö (1969). Stensiö (1969) noted the similarity of this pattern to the segments of diverse lepidotrichia seen in teleostomes.

Dorsal fins

There appears to be no evidence of a dorsal fin having been present in *H. westolli*. The submedian dorsal plate is absent and there appears to be no articulation preserved which would have attached fin radials to the vertebral column. There is also no evidence of fin rays or scales in the dorsal area suggestive of a fin. In addition there are several large rectangular scales which appear to have covered the area directly above the vertebral column (Fig. 2B and see description of scale type 2 below). These scales have a flat base, although they lack the tent-like structure of dorsal ridge plates. Similar, large rectangular scales are found in *Holonema radiatum* Obruchev, 1932 (= *Artenolepis golshanii* Janvier, 1974). In placoderms the presence of dorsal ridge plates tends to indicate the absence of a dorsal fin (Denison 1978).

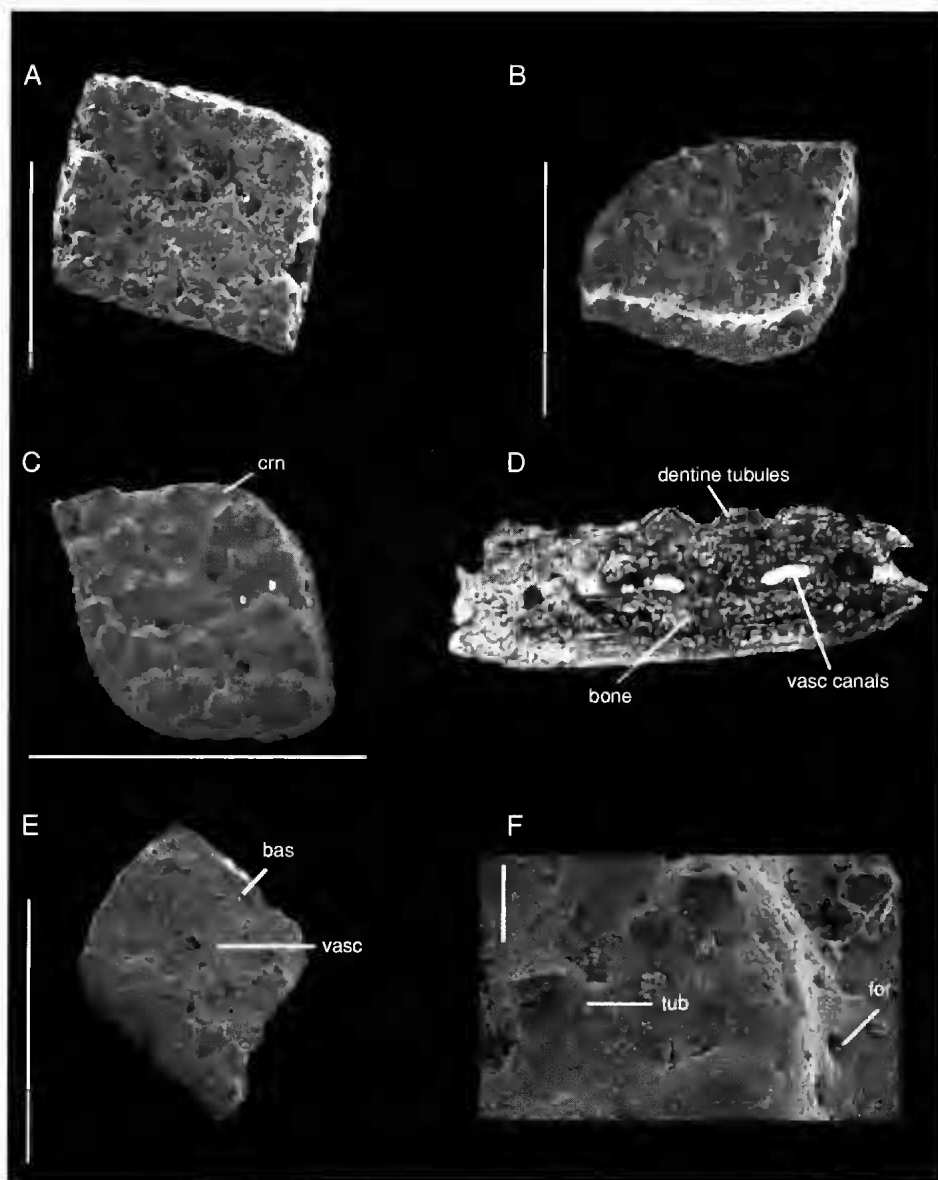


FIG. 6. — *Holonema westolli* (WAM 96.12.2); A, anterior body scale in crown view; B, lateral line scale in crown view; C, caudal scale in crown view; D, lateral thin section of anterior body scale; E, caudal scale in basal view; F, ornament of a caudal scale; **bas**, base of scale; **crn**, crown; **for**, foramina; **tub**, tubule; **vasc**, vasc canals, vascular canal; Scale bars: A-E, 1 mm; F, 0.01 mm.

Caudal fin (Fig. 2A, B)

The caudal fin of *H. westolli* is incompletely preserved. An impression of the anterior portion of the fin can be determined, however this gives little indication of the shape. The vertebral elements in the caudal region appear to turn upwards towards the dorsal lobe (Fig. 2A, B).

There appears to be no fin radials preserved.

Remarks. The caudal fin is interpreted as being heterocercal because the posterior caudal vertebrae turn upward towards the dorsal lobe, however these vertebral elements may merely be displaced in this position. In the eubranchyothoracids, the tail is slightly heterocercal with the hypochordal lobe

indicated by an elongation in the haemal spines at the base of the tail (Denison 1978).

SCALE DESCRIPTION

Scale type 1 (Fig. 6A-F)

The body behind the trunk shield is covered by small, rhombic, non-overlapping scales arranged in a pavement pattern (Fig. 2A). The anterior body scales are 1.3 mm long, 1.0 mm wide and 0.2 mm high (Fig. 6A). The scales decrease in size caudally (Fig. 6C) and towards the fin margins as in *Remigolepis* Stensiö, 1931 (Stensiö 1931). There are polygonally-shaped scales at the pelvic fin bases and these change to diamond shaped scales towards the fin margins. The crowns and bases of most scales are the same size with narrow grooves separating them (Fig. 6A, C). In addition there are a small number of quadrangular scales with a distinct neck, the base being wider than the crown (Fig. 6B). Similarly shaped scales from *H. radiatum* have been interpreted as lateral line scales (Goujet, pers. comm. 1997). The crown of each scale is covered with a variable number of sloping smooth tubercles placed well apart (Fig. 6F). The slope of each tubercle is uniformly orientated in a dorso-caudal direction with the caudal margin twice as high as the anterior margin (Fig. 6F). The tubercles of anterior scales are more closely positioned than caudal scales. The basal margin of the tubercles have a scalloped outline. The tubercles are incised anteriorly by up to six grooves separated by four ridges (Fig. 6F). Between the tubercles are numerous foramina which do not penetrate the convex, bony base (Fig. 6A-C, E-F). The side faces of the scales are always concave with numerous openings for vascular canals. There is a large vascular opening on the basal face of the scale with a variable number, up to ten, smaller vascular openings surrounding it (Fig. 6E). The vascular openings are usually located in the central part of the base.

Histology. The scales consist of two layers, a thick basal layer and a superficial ornamental layer (Fig. 6D). The bony base consists of laminated bone which contains numerous stellate bone-cell lacunae. There are numerous short cross-cutting fibres within the laminae. Within

the bases, there are also short intralamellar fibres, similar in structure to those in the bone bases of *Ohioaspis* (Wells 1944). There are large vascular canals within the bony base. The tubercles sit on the upper surface of the base. Within the tubercles are numerous branched semidentine tubules which have not retreated to the vascular canals. The main tubules are orientated perpendicular to the surface. Distally the tubules are straight and unbranched, closer to the lacunae they are interconnected by small multi-directional lacunal processes.

Remarks. The scales of *H. westolli* resemble the scale cover of *Selenosteus kepleri* Dean, 1901 and *Coccosteus cuspidatus* Miller, 1841 in their general form and in the absence of overlap zones. However, they differ from these placoderms because they are arranged in a definite pattern, regularly on the skin (Fig. 2A). The absence of a spongiöse layer, which is characteristic of placoderm endoskeletal bone, has been interpreted by Stensiö (1969) as representing a regressive state. Stensiö (1969) and Gross (1961) report the scales of *Lunaspis heroldi* Broili, 1929 show dorsal, lateral and ventral variation however, there appears to be little variation in the scale morphology in *H. westolli*. The trunk scales are rhomboid whereas the pelvic fin marginal scales are polygonal. The small degree of scale variation in *H. westolli* is similar to the condition in *Goodradigbeeon australium* White, 1978.

Scale type 2

These scales, located along the vertebral axis (Fig. 2B), are approximately three times larger than the body scales. They are rectangular in shape with a flat bony base separated from the crown by a narrow groove. They do not differ in ornament from scale type 1. Their increased size and their small number relative to other scales recovered from the specimens suggest they were median dorsal scales.

Remarks. These scales lack the pronounced crest present in the dorsal ridge scales of *Lunaspis*. Lelièvre *et al.* (1983, pl. 2, fig. 2) identified two types of scales from *Artenolepis golshanii* (= *Holonema radiatum*) and figure a long rectangular scale similar in morphology to the scales described for *H. westolli*.

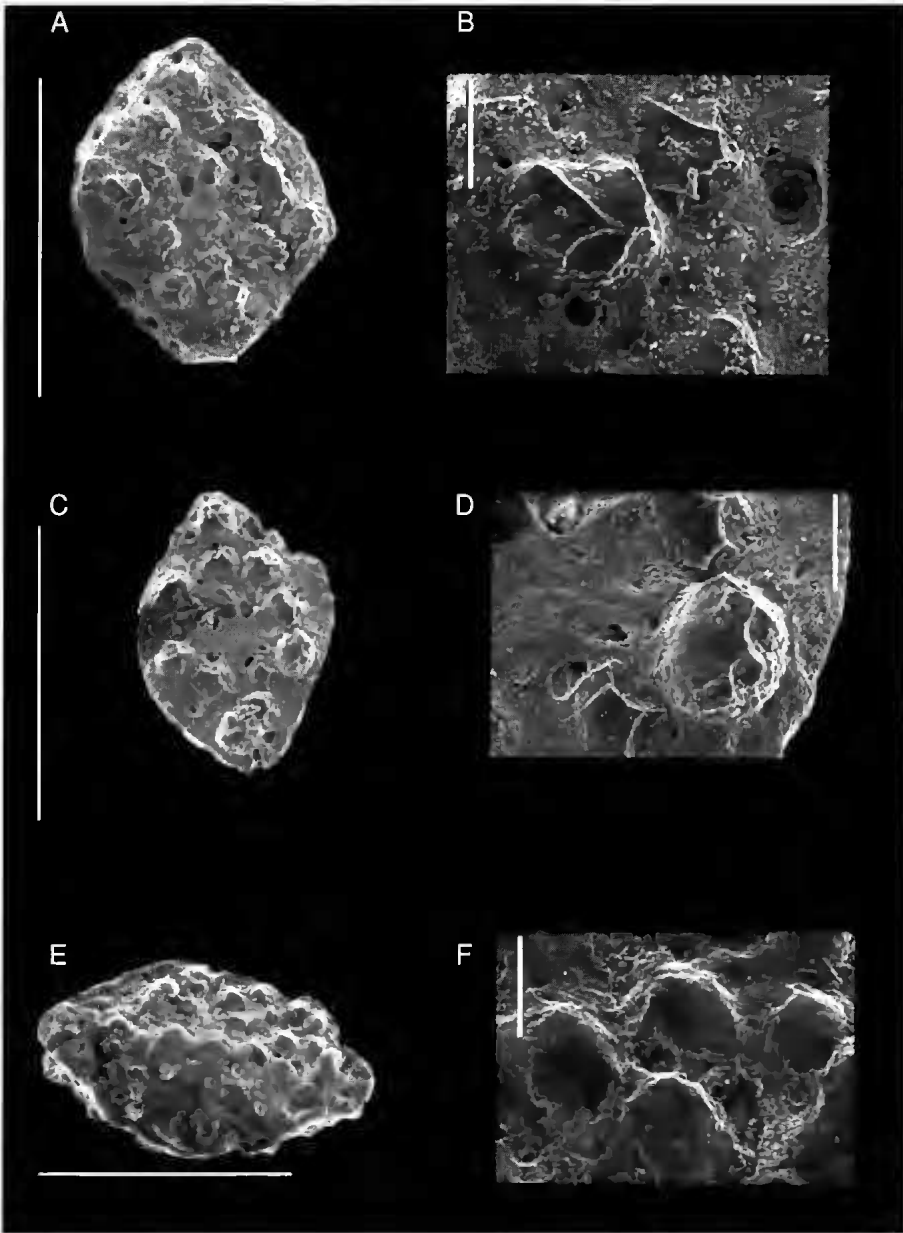


FIG. 7. — *Holonema westolli*; A, B, WAM 97.7.1; A, anterior body scale in crown view; B, detail of ornament; C, D, WAM 97.7.2; C, caudal body scale in crown view; D, detail of ornament. E, F, WAM 97.7.3; E, body sclae in crown view; F, detail of ornament. Scale bars: A, C, E, 1 mm; B, D, F, 0.1 mm.

FUNCTIONAL MORPHOLOGY OF *HOLONEMA WESTOLLI*

Denison (1978) states that most placoderms were not very powerful swimmers and Miles (1971) interpreted *H. westolli* as such. He based

these conclusions on the presence of an extensive trunk shield which he believed would limit the amount of musculature available for swimming. The recovery of the post-thoracic armour skeleton of *H. westolli* shows that this region was similar in size to the trunk armour and so there

appears to have been adequate musculature for an active mode of life. Large muscle contractions would not necessarily be needed to provide propulsion. The notocord, being a stiff but flexible rod, could have acted much like a tuning fork, with the energy from one unilateral contraction producing a resonant wave which decays. This method of providing caudal fin movement with a minimum of muscular energy is seen in extant *Xiphias* (Gill pers. comm.). Carr (1995) suggests that the inflexibility of the anterior part of the body would help to reduce the effects of yaw associated with primitive anguilliform swimming. The large pectoral fenestra is indicative of large pectoral fins (Miles 1971). Denison (1978) interpreted the large pectoral fins in *Pachyosteina* as efficient hydrofoils. Large pectoral fins provide lift and undulation of these fins can provide locomotion. In *H. westolli* the fins were positioned obliquely, with the anterior part of the fin being lower than the posterior part of the fin. A similar orientation of the pectoral fins is seen in modern sharks. In *H. westolli* the pectoral fins had a narrow fin base and so were probably not used for propulsion, instead they would have provided either passive or active lift, the amount of lift varying depending on the angle of the fin (Carr 1995). The pelvic fins are much smaller than the pectoral fins and properly acted more for balance and control.

The manoeuvrability of *H. westolli* has also been reinterpreted. Northcutt (1977) and Moss (1984) have shown that muscles attached to individual ceratotrichia in the heterocercal tails of extant sharks can independently change the lobe position and deliver thrust over a wide range of angles, not just forward and up, to produce differing hydrodynamic effects. The highly controllable heterocercal tail of living sharks allows them to develop extremely powerful dives and climbs in the water over a wide range of speeds. It is possible that *H. westolli* also had the ability to alter the shape of the caudal lobe thus providing it with an efficient means for moving up and down the water column.

In addition to having adequate swimming musculature *H. westolli* had a cambered body shape. This form of body shape performs hydrodynamically better than a spindled body shape

close to the sea bed as it decreases drag (Alexander 1967). However, cambering is only the ideal body shape in fishes that spend most of their active life in the layer of water immediately above the sea floor (Pridmore & Barwick 1993). It is therefore agreed with Miles (1971) that *H. westolli* was a benthic dwelling fish, although it is considered to have had an active swimming ability.

DESCRIPTION OF SCALES FROM THE GNEUDNA FORMATION

The availability of the almost complete tail region of *H. westolli* has enabled comparative study of the scales in relation to their position on the body of the fish, and from this, it is expected that the taxonomic significance of separate scales from the Gneudna Formation can be determined. Relatively abundant placoderm scale types have been recovered from residues of limestone from the Gneudna Formation and are referred to *H. westolli*. Larger plate and bone fragments of *Holonema* are found, but as yet, have not been studied. Because of the characteristic ornamentation of *Holonema*, these fragments can be attributed to the genus with some confidence.

DESCRIPTION

Scale type 1 (Fig. 7A-F)

Material. Thirty-one isolated scales.

Horizon. KT Beds 12, 14, 21a, 22 and OFB (Olegs Fish Bed) (Fig. 1).

The scales range in size from 0.2 mm to 1.5 mm long. They are relatively flat and do not possess a distinct neck or overlap margins (Fig. 6A, C, E). The ornament consists of a variable number of rounded tubercles, not more than fifteen per scale, with scalloped margins (Fig. 7B, D). The tubercles slope in a dorso-caudal direction with the caudal margin twice as high as the anterior margin. Interspersed amongst the tubercles are numerous foramina which however do not penetrate the base (Fig. 7B, D). The basal plate is flat to gently convex with one to four vascular canal openings located in the central part of the base. One small scale (unfigured) has been found and is considered to represent an ontogenetically

young scale. It is sub-oval, rather than rhombic in shape, with a central large tubercle surrounded by smaller tubercles.

Histology. The histological structure of the scales appears identical to that described for *H. westolli* from the Gogo Formation. The scales consist of a thick basal layer and a superficial tubercular layer that contains numerous branched semidentine tubules. The laminated bony base contains numerous stellate bone-cell lacunae. There are numerous short cross-cutting fibres within the laminae and short intra-lamellar fibres. There are large vascular canals within the bony base.

REMARKS

These scales have been referred to *H. westolli* after direct comparison with *in situ* scales of *H. westolli* from the Gogo Formation. They are distinguished from other placoderm scales by their flat or concave base, narrow neck groove, widely spaced tubercles and distinctive tubercular ornament. They differ from *H. radiatum* (Janvier, 1974) in having scalloped margins around the tubercular ornament, being relatively flat with an indistinct neck and the crown and basal plate being the same size.

AGE OF THE GNEUDNA FORMATION

The Munabia Sandstone is conformable on the Gneudna Formation and Long (1991b) considered the occurrence of *Holonema* and *Bothriolepis* Eichwald, 1840 together in the Munabia Sandstone as consistent with an early-middle Frasnian age for the Munabia Sandstone. Lelièvre (1981) also reports the association of *Holonema* and *Bothriolepis* as age indicators for the Frasnian of Turkey and Iran. In the Gneudna Formation *Bothriolepis* sp. is identified from KT Beds 14-15 based on a well-preserved right mesial lateral 2 plate, an anterior ventrolateral plate and an anterior dorsolateral plate (Long & Trinajstić in press) and *H. westolli* is recognised from isolated scales from KT Beds 12-14 and KT Beds 22 and OFB. Along with the *Holonema*/*Bothriolepis* association, the upper section of the Gneudna Formation has yielded some conodonts, with *Ancyrodella* (Nicholl 1979) considered to confer

a firm Frasnian age on the higher beds in the section. The presence of *Ancyrodella* indicates that the unit in which it occurs is no older than the lower *Polygnathus asymmetricus* Zone.

In addition to conodonts a number of macrofossils have recently been recovered from the Gneudna Formation which suggests the upper portion is contemporaneous with the early Frasnian Gogo Formation. Long (1985) referred a lungfish ascribed to *Dipterus* cf. *digitatus* Seddon, 1969 to *Cbirodipterus australis* Miles, 1977. A lower jaw lungfish tooth plate was found from KT Bed 22, which closely resembles a new taxon currently being described from the Gogo Formation by Prof. K. Campbell and Dr R. Barwick, and has been provisionally referred to this, as yet unnamed, taxon (Long & Trinajstić in press). In addition the macrofossil scales of the palaeoniscoid *Moythomasia durginga* Gardiner et Bartram, 1977 has been identified as occurring throughout the Gneudna Formation (Trinajstić 1997). The significance lies in that now that two dipnoan taxa, one placoderm taxon and one palaeoniscoid taxon found in the uppermost section of the Gneudna Formation are taxa also recorded from early Frasnian Gogo Formation. This supports the suggestion of Turner & Dring (1981) that the Gneudna Formation is lower Frasnian.

DISCUSSION

Of all the large brachythoracids, *Holonema* is reported to have had the widest distribution, being known from Middle and Upper Devonian rocks in North America, Europe (Janvier 1983; Lelièvre et al. 1990) the Middle East (Schultze 1973; Janvier 1977; Lelièvre et al. 1990) and Australia (Miles 1971; Long 1991). In Australia *Holonema* is known from the Frasnian Munabia Sandstone (Long 1991b) and Gogo Formation (Miles 1971). Until now *H. westolli* was thought to be endemic to the Gogo Formation, however its confirmed presence at the Gneudna Formation and possible presence in the Munabia Sandstone suggests that *H. westolli* was widely dispersed. Miles (1969) suggested the holonema-

tids had a broad adaptive zone and were thus suited for easy dispersal.

A recognized problem in using placoderms in biostratigraphic analysis is their reported endemism, particularly in Australia and China. With more Givetian and Frasnian strata being examined this perceived endemism is decreasing with three fish genera and two species, formerly considered endemic to the Gogo Formation, now occurring in the Gneudna Formation. The association of *Holonema* with placoderms such as *Groenlandaspis* Heintz, 1932 and *Bothriolepis*, which also have a recognized wide geographic distribution, may provide a tool for long-distance correlation between marine and non-marine stratigraphic sequences (Lelièvre & Goujet 1986).

In addition to questions of endemism are problems in the identification of species, especially when there are only isolated scales preserved. The squamation of *H. radiatum* was originally identified as *Artenolepis golshanii* (Janvier 1974) and it was not until these scales were found in association with *Holonema* cf. *radiatum* plates (Lelièvre *et al.* 1983) and these remains identified as *H. radiatum* (Lelièvre *et al.* 1990) that the scales were correctly attributed. Although Lelièvre *et al.* (1983) noted similarities in the crown ornamentation between *H. radiatum* and the phlyctaenioid arthrodire *Goodradigbeeon australianum* White, 1978 he was able to distinguish between the two species due to differences in the base and scale form in profile. The ability to distinguish between scales of *H. radiatum* and *H. westolli* has enabled the conclusion that there are species differences between holonematid scales. This suggests that placoderm species may be identified from scales and that greater utilization of placoderm scales will be possible in future biostratigraphic works.

SUMMARY AND CONCLUSIONS

1. The species *Holonema westolli* Miles, 1971 is redescribed from a new specimen showing it to have a vertebral column composed of paired elements without neural or haemal arches, a dermal scale cover, semi-circular pelvic fins located

directly behind the posterior ventral plate and a pelvic girdle with no basal plate.

2. The scales of *H. westolli* can be distinguished from *H. radiatum* and other known placoderm scales and so are useful in diagnosis and have potential in biostratigraphic correlation.

3. By direct comparison, both morphological and histological, isolated scales recovered from residues from the Gneudna Formation have been referred to *H. westolli*, extending the range of the species in Western Australia.

4. The presence of *H. westolli* in the Gneudna Formation has brought the number of fish species also present in the Gogo Formation to two and genera to three, supporting an early Frasnian age for the Gneudna Formation.

Acknowledgements

Many thanks are owed to Drs Kim Dennis-Bryan and Daniel Goujet who assisted greatly with this work and in the preparation of the manuscript. I must also thank Carole Burrow and Ross Parkes for their patience in teaching me some histology and thin sectioning. Thanks also to Mr. Geoff Deakin from UWA who took the photographs and Dr David Haig who read early drafts. My thanks to the three reviewers of this paper, Dr P. Janvier, Dr H. Lelièvre and Dr A. Ohler for their helpful comments. I am indebted to Dr J. Long for permission to work on the Gogo material and to the Percy family of Williambury Station who granted permission for collecting additional material on their property.

REFERENCES

- Alexander R. M. 1967. — *Functional Design in Fishes*. Hutchinson, London, 160 p.
- Broili F. 1929. — Acanthospiden aus dem rheinischen Unterdevon. *Akademie der wissenschaften und der Literatur in Mainz. Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse (Wiesbaden)* ABT 2: 143-63.
- Burrow C. J. 1996. — Placoderm scales from the Lower Devonian of New South Wales, Australia. *Modern Geology* 20: 351-369.
- Carr R. 1995. — Placoderm diversity and evolution. in Arsenault M., Lelièvre H. & Janvier P. (eds), *Studies on Early Vertebrates (VIIth International Symposium, 1991, Miguasha Parc, Quebec)*,

- Bulletin du Muséum national d'Histoire naturelle*, Paris, série 4, 17 C (1-4) : 85-125.
- Dean B. 1901. — Further notes on the relationships of the Arthrognathi. *Memoirs of the New York Academy of Sciences* 11: 110-123.
- Denison R. H. 1978. — Placodermi in Schultze H-P. (ed.). *Handbook of Paleichthyology*. Part 2. Gustav Fischer Verlag, Stuttgart, 128 p.
- Dennis K. D. & Miles R. S. 1979. — A second eubrachythoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 67: 1-27.
- Dennis K. D. & Miles R. S. 1981. — A pachyosteor-morph arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 73: 213-258.
- Dennis-Bryan K. D. 1987. — A new species of east-manosteoid arthrodire (Pisces, Placodermi) from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 90: 1-64.
- Gardiner B. G. & Bartram A. W. H. 1977. — The homologies of ventral cranial fissures in osteichthyans: 227-245, in Andrews S. M., Miles R. S. & Walker A. D. (eds), *Problems in Early Vertebrate Evolution*. Academic Press, London.
- Gardiner B. G. & Miles R. S. 1990. — A new genus of eubrachythoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 99: 159-204.
- 1994. — Eubrachythoracid arthrodires from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 112: 443-477.
- Goujet D. 1973. — *Sigaspis*, un nouvel arthrodire du Dévonien inférieur du Spitzberg. *Palaeontographica* 143A: 73-88.
- Gross W. 1961. — *Lunaspis broilli* und *Lunaspis heroldi* aus dem Hunsruckscheifer (Unterdevon; Rheinland). *Notizblatt des bessisches Landesamt für Bodenforschung*. Weisbaden 89: 17-43.
- Janvier P. 1974. — Preliminary report on Late Devonian fishes from central Iran. *Geological Survey of Iran Reports* 31: 5-48.
- 1977. — Les Vertébrés Dévoniens de l'Iran central et de l'Afghanistan. *Mémoires de la Société géologique du France* 8 : 277-289.
- 1983. — Les vertébrés dévoniens de la nappe supérieure d'Antalya (Taurus Lycien occidental, Turquie). *Géologie Méditerranéenne* 10 (1) : 1-13.
- Lelièvre H., Goujet D. & Morzadec P. 1983. — Les poissons du Frasnien (Dévonien supérieur) de Traonlions en Plougastel-Daoulas (Bretagne Occidentale). *Bulletin de la Société géologique et minéralogique de Bretagne* 15 : 75-83.
- Lelièvre H. & Goujet D. 1986. — Biostratigraphic significance of some uppermost Devonian placoderms. in Bless M. J. M & Streef M. (eds). Late Devonian events around the Old Red Continent (Aachen, 1986). *Annales de la Société Géologique de Belgique* 109 (1) : 55-59.
- Lelièvre H., Goujet D. & Henn A. 1990. — Un nouveau spécimen d'*Holonema radiatum* (Placodermi, Arthrodira) du Dévonien moyen de la région d'Orviedo, Espagne. *Bulletin du Muséum national d'Histoire naturelle*, Paris, série 4, C 12 (1) : 53-83.
- Long J. A. 1985. — A new osteolepidid fish from the Upper Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum* 12: 361-377.
- 1988. — A new camuropiscid arthrodire (Pisces: Placodermi) from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 94: 233-258.
- 1991a. — The long history of fossil fish: 336-428, in Vickers-Rich P., Monaghan J. N., Baird R. F. & Rich T. H. (eds). *Vertebrate Palaeontology in Australasia*. Pioneer Design Studios with Monash University Publications Committee, Melbourne.
- 1991b. — Devonian fish remains from the Munabia Sandstone, Carnarvon Basin, Western Australia. *Records of the Western Australian Museum* 15 (3): 503-515.
- 1995. — *The Rise of Fishes*. University of New South Wales Press and John Hopkins University Press, Sydney.
- Long J. A. & Trinajstić K. M. (in press). — An overview of the Devonian microvertebrate faunas of Western Australia. *Courier Forschungsinstitut Senckenberg*.
- Miles R. S. 1969. — Features of placoderm diversification and the evolution of the arthrodire feeding mechanism. *Transactions of the Royal Society of Edinburgh* 68: 123-170.
- 1971. — The Holonematidae (placoderm fishes): a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of London* 263 B: 101-234.
- 1977. — Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society* 61: 1-328.
- Miles R. S. & Westoll T. S. 1968. — The placoderm fish *Cocosteus cuspidatus* Miller ex Agassiz from the Middle Old Red Sandstone of Scotland. Part 1. Descriptive morphology. *Transactions of the Royal Society of Edinburgh* 67: 373-476.
- Miller H. 1841. — *The Old Red Sandstone; or new walks in the old field*. Johnstone, Edinburgh, xxiii + 275 p.
- Moss S. A. 1984. — *Sharks: an Introduction for the Amateur Naturalist*. Prentice-Hall, Englewood, 150 p.
- Nicholl R. 1979. — *A Late Devonian age for the Munabia Sandstone, Carnarvon Basin, W.A.* Australian Bureau of Mineral Resources, Professional Olinion Geology 79/034 (unpublished).
- Newberry J. S. 1873. — The classification and geological distribution of our fossil fishes. *Reports of the*

- Geological Survey of Ohio, Columbus* 1(2): 245-355.
- Newberry J. S. 1889. — The Palaeozoic Fishes of North America. *United States Geological Survey, Monograph* 16: 340 p.
- Northcutt R. G. 1977. — Recent advances in the biology of sharks. *American Zoologist* 17: 2.
- Obrutchev D. 1932. — Holonematidae des Russischen Devons. *Travaux de l'Institut de paléozoologie*, Académie des Sciences, URSS 2 : 97-115.
- Pridmore P. A. & Barwick R. E. 1993. — Post-cranial morphologies of the Late Devonian dipnoans *Griphognathus* and *Chirodipterus* and the locomotor implications. *Memoirs of the Association of Australasian Palaeontologists* 15: 161-182.
- Rixon A. 1979. — *Fossil Animal Remains, Their Preparation and Conservation*, Athlone Press, London, 375 p.
- Schultze H.-P. 1973. — Large Upper Devonian arthrodiros from Iran. *Feldiana Geology* 23: 53-78.
- Seddon G. 1969. — Conodont and fish remains from the Gneudna Formation, Carnarvon Basin, Western Australia. *Proceedings of the Royal Society of Western Australia* 52: 21-30.
- Stensiö E. A. 1931. — On the Upper devonian vertebrates of East Greenland. *Meddelelser om Gronland* 86: 1-212.
- 1969. — Elasmobranchiomorphi, Placodermata Arthrodiros: 71-692, in Piveteau J.-P. (ed.), *Traité de Paléontologie*. Masson, Paris.
- Trinajstić K. M. 1997. — The biostratigraphic importance of isolated scales from Devonian palaeoniscoids. *Conference of Australasian Vertebrate Evolution, Palaeontology and Systematics*, Abstracts Volume: 21.
- Turner S. & Dring R. S. 1981. — Late devonian thelodonts (Agnatha) from the Gneudna Formation, Carnarvon Basin, Western Australia. *Alceberinga* 5: 39-48.
- Turner S. & Murphy M. A. 1988. — Early devonian vertebrate microfossils from the Simpson Park Range Eureka county, Nevada. *Journal of Paleontology* 62: 959-964.
- Watson D. M. S. 1934. — The interpretation of arthrodiros. *The Proceedings of the Zoological Society of London*: 437-464.
- Wells J. W. 1944. — Fish remains from the Middle Devonian Bone Beds of the Cincinnati Arch region. *Palaeontographica Americana* 3: 989-160.
- White E. I. 1978. — The larger arthrodiran fishes from the area of Burrinjuck Dam, NSW. *Transactions of the Zoological Society of London*. 34: 149-262.
- Young G. C. 1974. — Stratigraphic occurrence of some placoderm fishes in the Middle and Upper Devonian. *Newsletter of Stratigraphy* 3, 4: 243-261.

*Submitted for publication on 11 December 1997;
accepted on 19 May 1998.*